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General and Specific Mechanisms of Biochemical Interactions between Plants*

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Abstract. There exist two main mechanisms of allelopathy: 1) direct transfer of metabolites between neighbouring plants during their life and 2) accumulation and transformation of bioactive substances in the environment with their subsequent influence on higher plants. The latter mechanism is similar to that causing soil sickness or soil toxicity. Allelochemicals affect all functions of the living system: photosynthesis, respiration, mineral nutrition, transpiration, immunity, and growth. The initial biochemical effect of allelochemicals seems to be on the synthesis of protein mediated by RNA/DNA. Knowledge of the mechanisms of concrete signals during realization of hereditary codes would serve as a powerful tool for the improvement of crop plant development and productivity.

The concept of "mechanism", which initially appeared in mechanics, has in recent decades become widely used in other spheres of science, including biochemistry. In mechanics, this term denotes a system of bodies that is able to transform the motion of a single body or several bodies into resultant motion of other bodies. Bodies thus interacting are called components and form a kinematic couple. Applying the term mechanism to allelopathy, *i.e.* to various processes of interaction between higher plants mediated by physiologically active substances called allelochemicals, we mean that components of interaction here are the donor plant and the acceptor plant while allelochemicals serve as the kinetic liaison between them.

In Fig. 1, the general mechanism of allelopathy is represented as we see it. The donor is the generating plant; the acceptor, or recipient, plant is subjected to the action of substances emitted from the donor. Clearly, where a pair of plants is involved, each one may be both the donor and the acceptor simultaneously.

On the way from the donor plant, the emitted substances may be partly resorbed, *i.e.* taken up again by the plant that liberated them, or subjected to diverse transformations due to abiogenic factors (light, oxygen, *etc.*) and heterotrophic

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* This paper is based on and employs a broader definition of allelopathy than most other contributions to this collection of colloquium reports, in that it includes all interactions of plants, not merely inhibitory ones.

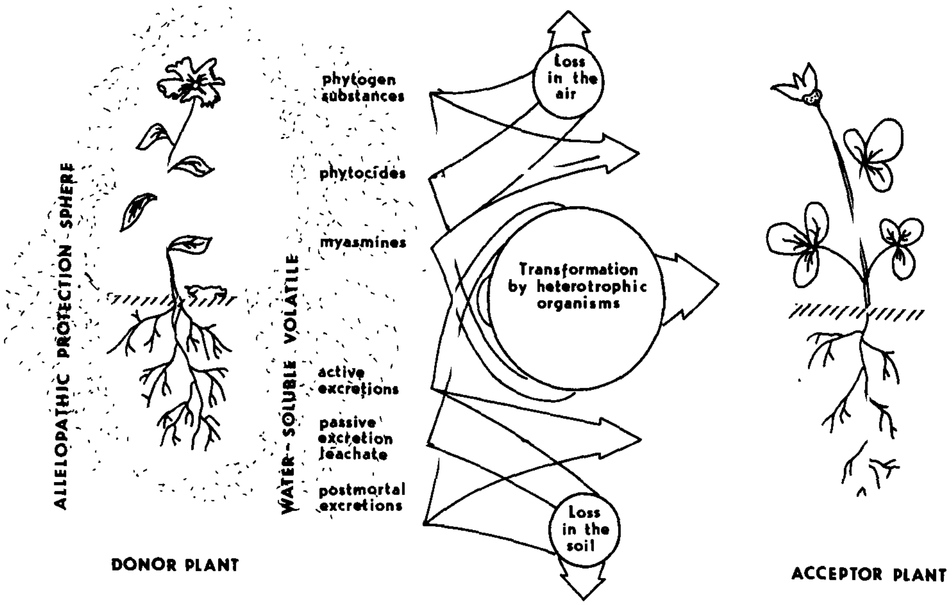

Fig. 1. Allelopathic cycling.

organisms. Some of the organic excreta may reach a neighboring plant without any changes.

The mechanisms of interaction may be differentiated according to the levels of the hierarchic organization of living beings : see Table 1.

The intracellular mechanisms of allelochemical action involve various aspects of metabolism and in fact do not differ from other biochemical mechanisms except that in the case of allelopathy we rarely deal with pure substances. Normally, a great variety of components enter the active allelochemical complexes. Therefore, their effect is usually nonspecific: where low concentrations and unprolonged action are involved, all processes are stimulated, while with higher concentrations and longer activity, life activity is suppressed and ceases. In Fig. 2 the nonspecific effect of allelochemicals is shown.

On the organism level, allelopathic effects are exhibited in various complicated physiological processes, for instance, in photosynthesis (MOKHOVA 1965, KOLESNICHENKO 1971), respiration and nutritional uptake (FILIPPOVICH 1966), growth (RICE 1984), plant productivity (CHERNOBRIVENKO 1956), stress resistance (LAŠTŮVKA 1986), and quality of plant production (GRODZINSKY 1973).

On this level, the main interest seems to be in the mechanism of allelopathic effects on the phenotype. BARANETSKY and MOROZ (1988) suggested that allelochemicals may play the role of genome suppressors or repressors, affecting in this way the deciphering and utilization of genetic information in the recipient plant growth. Evidence in support of this mechanism still has to be found but it seems plausible.

TABLE 1
Hierarchical organization of living organisms

Level of action of the substance	Substances carrying information	Objects connected	Science concerned
From biological macro-molecule to organelles of the cell	Specific metabolites, t-RNA, enzymes, repressors	inside the cell	Molecular biology
From cell to tissue or organ	Enzymes, vitamins	cells and tissues	Biochemistry (enzymology)
From organ to whole organism	Phytohormones, auxins, inhibitors, retardants	organs	Physiology (endocrino-logy)
Phytocoenosis (biogeocoenosis)	Allelochemicals, anti-biotics, phytocides, telergones, teletoxins	organisms	Allelopathy

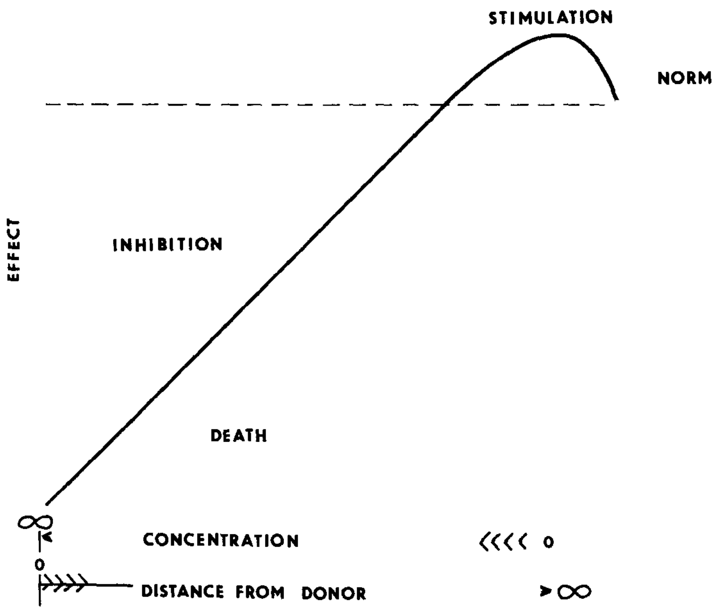

Fig. 2. Relation between concentration (or distance from donor to acceptor plant) and the physiological effect of active substances.

On the whole, of the greatest interest in allelopathy are investigations into coenotic, or ecological, mechanisms, *i.e.* interactions occurring on the phytocoenotic level (ecosystem). These mechanisms can be divided into two main groups, as follows.

ACTIVE METABOLITE EXCHANGE

As shown in experiments with ^{14}C-labelled CO_2, assimilate exchange between neighboring plants occurs rapidly and extensively (IVANOV 1973) through roots. The products of photosynthesis can be found in adjacent plants 6–12 h after exposure to light; the amount of transported products may reach 8–12 percent of the overall products of photosynthesis. Obviously, the largest part of the exchanged products are sugars, amino acids, other organic acids, *etc.* that are common to all plants. Therefore, such exchange purely concerns energy value. In particular, DZIUBENKO *et al.* (1975) indicated that the assimilates of maize are accumulated in large quantities in the tubercles on nearby legume roots, thus enabling participation of the maize in nitrogen fixation.

In experiments we conducted, the assimilates of cultivated plants were absorbed during droughts by weeds while no exchange occurred in the opposite direction (GRODZINSKY 1978). Thus, it is evident that weeds rob cultivated plants in this way, too.

TABLE 2
Interaction between crop and weed plants in sand culture (fresh mass of 20 plants)

Test species and their combinations	30-day-old plants			86-day-old plants		
	shoot mass		root mass	shoot mass		root mass
	[g]	[%]	[g]	[g]	[%]	[g]
Maize alone	128.80	100	27.30	350.0	100	186.60
Pigweed (*Amaranthus retroflexus*) alone	70.00	100	6.80	341.66	100	25.50
Lamb's quarters (*Chenopodium album*) alone	75.60	100	6.14	241.66	100	33.00
Pigweed mixed with maize	10.86	15.4	1.14	43.80	12.8	3.66
Lamb's quarters mixed with maize	13.28	17.40	0.80	55.00	22.8	7.16
Maize mixed with pigweed	176.00	143.00	33.04	388.80	119.00	222.00
Maize mixed with lamb's quarters	236.00	191.00	38.40	522.20	149.00	244.40

However, specific compounds are also frequently transported, producing a tangible effect on the metabolism of neighbouring plants. For instance, in the experiments conducted by DZYUBENKO and PETRENKO (1971) and DZYUBENKO *et al.* (1975), during combined growth of cultivated and weed plants, the total mass of plant roots differed considerably as compared to controls (Table 2).

KHOLODNY (1957) demonstrated absorption of organic volatiles by the cut-off roots of maize, legumes, and sunflower that made their life twice as long as that of controls, and increment in length was also observed. He likewise demonstrated the possibility of an excellent growth of colonies of microorganisms due to plant volatile substances on an otherwise barren substrate (KHOLODNY 1944, 1948).

Regrettably, the process of metabolite exchange is thoroughly neglected both in agricultural investigations and their practical applications, although evidence exists that this exchange favorably affects the protein contents in forage, improves taste qualities of fruits and vegetables, increases resistance against pests and diseases, benefits the bouquet of wines, *etc.*

SUBSTRATE SICKNESS

The second numerous group of allelopathic mechanisms is characterized by an additional constituent – an intermediate accumulation of allelochemicals in the substrate, where they either gradually reach the level that is toxic for plants or undergo various transformations. They are supplemented by the metabolites of microorganisms or products of physicochemical transformations of waste matter from living plants or dead plant bodies. This intermediate mechanism is none other than the initial stage of humus formation when in the substrate there exist low-molecular products, mainly of phenolic nature, which are then transformed into humus.

Some typical examples of this group, of the many that could be cited, are given below.

1. In some instances the living plants produce allelochemically active substances that can inhibit the growth of plants of the same or different species. For example, allelochemicals are present in many fruits; if these remain where they fall and are not eaten by animals, they may block germination of seeds and development of seedlings of competitors. This has been studied *e.g.* by GRODZINSKY *et al.* (1960, 1978) for *Crambe tatarica* SEBEÖK, GRODZINSKY (1965) for *Adonis wolgensis* STEV., and WALLER *et al.* (1986) for *Coffea arabica* L. Similar effects have been reported for terpenes produced by *Salvia leucophylla* (MULLER and MULLER 1965) and *Eucalyptus* species (DEL MORAL and MULLER 1964) that are adsorbed in soil and accumulate there. Rain drops or dew wash down phytotoxic substances from the leaves of various plants (TUKEY 1971). Much earlier the toxicity of some root exudates to plants of the same or different species was reported (SCHREINER and REED 1907).

In other cases living plants liberate volatile allelopathic chemicals to the atmosphere, which diffuse to surrounding plants and damage or kill them. This has been observed *e.g.* for terpenes from *Salvia* species (MULLER and MULLER 1964, MULLER 1965), emanations from various desert plants (FRIEDMAN 1987), and volatiles from the unicorn plant (*Proboscidea louisianica*) that are toxic towards cotton (*Gossypium hirsutum*).

2. Another mechanism of production of allelochemicals is the action of microorganisms on leaf litter and other plant remains. This, along with toxins from unconverted plant residues, is the commonest cause of so-called soil sickness: It occurs when a plant species is grown generation after generation on the same ground. Under natural conditions, plants that cause soil sickness lead a nomadic mode of life, migrating to new places or growing as solitary individuals, where they do not produce a toxic effect in the soil. In agriculture, however, this allelopathic phenomenon is the most widespread and economically important (Fig. 3). Particularly severe intoxications were observed when apple trees were planted after apple trees, peaches after peaches, and citrus after citrus (SCHANDER 1956). Thus, when large quantities of post-yield remains, as of wheat, or other undecomposed organic matter are introduced into soil, the fungi that destroy them produce phytotoxic substances

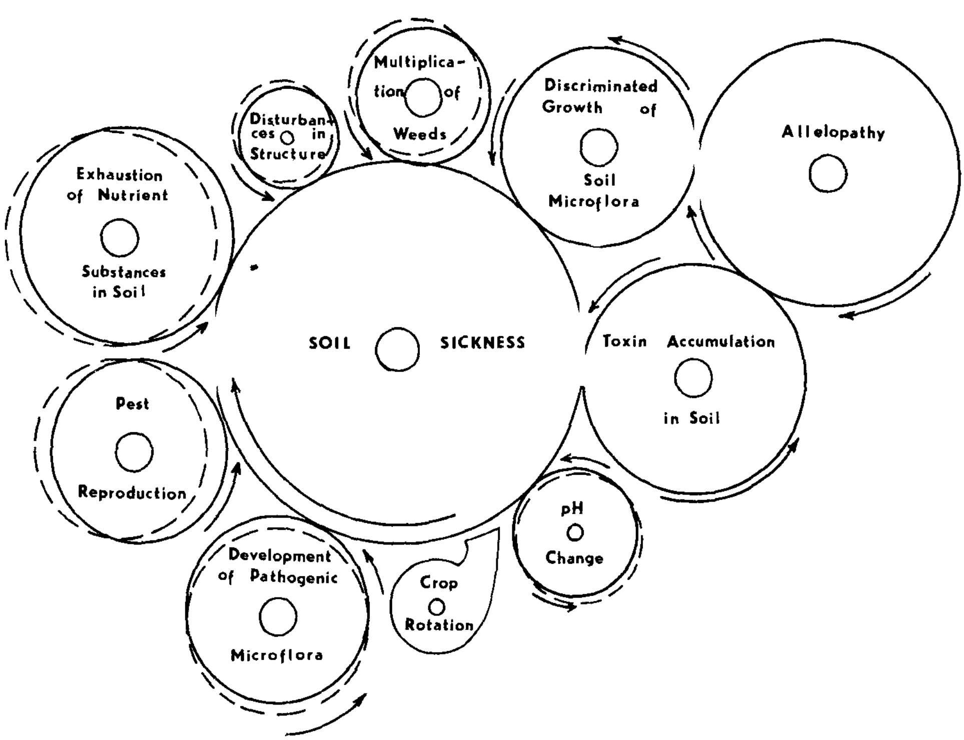

Fig. 3. Scheme of allelopathic phenomena involved in soil sickness.

(MCCALLA 1971). The anaerobic conditions that prevail when fields of rice or sugar cane are flooded promote formation of alcohols, keto acids, and a number of reduced compounds that as a rule are toxic for higher plants (WANG 1967).

3. VIVRETT and MULLER (1977) showed that ice grass accumulates large quantities of salts and after death leaves them in the upper layer of the soil, making it worthless for the cultivation of salt-susceptible species. A similar mechanism was earlier described by BYKOV (1961) for Asiatic poplar and Middle Asian tamarisk.

4. RICE (1984) found some depression of the processes of nitrogen fixation and nitrification by allelochemicals of higher plants. Therefore, in a number of cases, the damage is carried out not by the direct effects of allelochemicals but indirectly, through a decreased level of available nitrogen.

5. Indirect allelochemical effects can also be due to participation of animal herbivores whose excrements exert toxic influences on plants. This was described by TRENBATH and FOX (1977) for *Chrysoptarta m-fuscus* on *Eucalyptus globulus*, and by BUKOLOVA *et al.* (1978) for aphids on *Tilia cordata*.

6. A peculiar mechanism has been observed in the tundra zone: lichens, especially *Cladonia alpestris*, excrete antifungal substances that suppress mycorrhizal development on pine roots and thus cause a sharp decrease of phosphorus nutrition. The growth of mycorrhiza is inhibited for decades, until the lichens under the tree canopy are entirely exterminated (BROWN and MIKOLA 1974).

7. Since the soil contains colloids, variations in their hydrophysical properties due to the effects of allelochemicals may considerably improve or depress the soil water-retaining ability and thereby affect plant growth. For example, the oak increases hydrophilic properties of soil while the ash tree decreases them. Accumulation of lipophilic products in the soil was reported as early as the beginning of the 20th century. They were called soil wax, "agricera", and shown to interfere with water uptake by the soil (SCHREINER and REED 1907).

DISCUSSION

Adverse allelopathic mechanisms are assignable to the physiological effects of toxic substances (sometimes called cholines) on the growing plant. The plant is believed to be forced to absorb these substances and is intoxicated by them if they are sufficiently abundant. This can be fairly well demonstrated in bioassays in which the seeds of a rapidly growing species, or their parts, are exposed to a solution or gas mixture under investigation, and have no alternative to a direct dynamic reaction to these substances.

As has been shown in the aforementioned examples of allelopathy, similar reactions are observed in nature. It is manifested either in stimulation or suppression of plants and, as was indicated earlier, is nonspecific in character.

However, it should be noted that in natural communities occupying some successional stage, when their composition was forming during a very long, often geological, period of time, the interrelations between individual components or various species were subjected to evolutionary modifications. Allelopathic phenomena should not be narrowly treated from this standpoint only. Numerous observations give evidence of the survival of seeds, bulbs, tubers, and rootstocks in soil for many years if the environmental situation is unfavorable for their growth. In contrast to the above-illustrated dynamic reaction, the latter can be called the static reaction : plants react to an allelopathic factor by suspension of growth and transition into cryptobiosis, as if awaiting favorable phytocoenotic conditions.

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